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PARTITIONING AND SHARING OF POLLINATORS BY FOUR SYMPATRIC SPECIES OF *DALECHAMPIA* (EUPHORBIACEAE) IN PANAMA¹

W. SCOTT ARMBRUSTER² AND ANN L. HERZIG³

ABSTRACT

Observations were made on distribution, floral morphology, and pollination of four species of *Dalechampia* (Euphorbiaceae) in central Panama. The four species occur sympatrically in various combinations throughout Panama and are pollinated by resin-collecting euglossine bees, and resin- and/or pollen-collecting stingless bees and megachilid bees. With one exception, these plant species overlap very little in pollinators or time of pollination. *Dalechampia heteromorpha* is pollinated early in the day by *Trigona* and *Hypanthidium* whereas a sympatric congener, *D. scandens*, is pollinated by the same species of bees late in the day. A third sympatric species, *D. dioscoreifolia*, is pollinated by euglossine bees. *Dalechampia heteromorpha* also occurs sympatrically with *D. tiliifolia*; the latter is pollinated by euglossine bees. Individuals of *Dalechampia dioscoreifolia* and *D. tiliifolia* were observed occurring together at only one site; here they shared pollinators (euglossine bees) and were receptive to pollination at the same time of day. Interspecific pollen flow was substantial and may have resulted in depressed seedset in *D. dioscoreifolia*.

A number of authors have suggested that plant communities are likely to be organized in ways that minimize reproductive interference (Levin, 1970; Levin & Anderson, 1970; Mosquin, 1971; Straw, 1972; Reader, 1975; Heinrich, 1975). [We here define the term "reproductive interference" to include all plant-plant interactions that have direct detrimental effects on reproductive processes, including competition for pollinator service, interspecific pollen transfer, and competition for agents of seed dispersal; this is more

inclusive than the phrase "competition for pollination" used by Waser (1982).] There have been a number of studies that indicate such organization occurs in natural communities (Snow, 1966; Frankie, 1975; Reader, 1975; Heinrich, 1976a; Stiles, 1975, 1977; Feinsinger, 1978; Waser, 1978a; Brown & Kodric-Brown, 1979; Parrish & Bazzaz, 1979). However, as several authors have pointed out, before claiming that organizing processes have affected community structure it is necessary to show statistically that

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² Department of Botany, University of California, Davis, California 95616. Present address: Department of Biology, Fisheries and Wildlife and Institute of Arctic Biology, University of Alaska, Fairbanks, Alaska 99701.

³ Institute of Northern Forestry, USDA Forest Service, 308 Tanana Dr., Fairbanks, Alaska 99701.

niche overlap in a community is less than that of a randomly generated assemblage of species (Connor & Simberloff, 1979; Poole & Rathcke, 1979; Strong et al., 1979). Further, as Grant (1972), Roughgarden (1976), Feinsinger (1978), Slatkin (1980), Waser (1983), and others have pointed out, the observed organization may be either the result of evolution of the component species in response to their biotic environments or the result of the sorting of preadapted species into "compatible" associations. It is difficult, at best, to distinguish between these two processes.

These limitations notwithstanding, we believe that it remains useful to investigate the ecological relationships between members of species assemblages. While detailed studies of a single community usually cannot demonstrate community organization, they may reveal the selective pressures that have been operating and the "cost" of not being adapted to sympatry.

We have been interested in how assemblages of sympatric species of *Dalechampia* (Euphorbiaceae) are organized, especially with respect to use of the pollinating fauna and to potential interspecific pollen flow. The pollination systems of three different pairs of sympatric species of *Dalechampia* in South America and Mexico have been discussed by Armbruster and Webster (1979, 1981, 1982). In each case the pollinators were effectively partitioned, and there was very little interspecific pollen flow. In this paper we describe the relationships between four species of *Dalechampia* (*D. dioscoreifolia*, *D. heteromorpha*, *D. scandens*, and *D. tiliifolia*) that occur in several combinations of sympatry in Panama and examine the relationships with pollinators, the extent of resource partitioning, and the amounts of interspecific pollen flow.

Dalechampia contains about 100 species, most of which are small to moderate-sized lianas of lowland neotropical habitats. All species are monoecious; the unisexual flowers are grouped together into functionally bisexual pseudanthial inflorescences (Webster & Webster, 1972). In most species studied, including those considered here, the inflorescence contains three pistillate flowers, 8–13 staminate flowers, and a gland-like structure that secretes resin (Armbruster & Webster, 1979). The whole inflorescence is subtended by two usually large and showy bracts.

In most species of *Dalechampia*, including the subjects of this study, the pistillate flowers are receptive several days prior to anthesis of the staminate flowers in the same inflorescence. Sub-

sequently there is a bisexual phase during which the pistillate flowers are still receptive, but the staminate flowers are also open and pollen is being shed. During the bisexual phase self-pollination may occur; since all *Dalechampia* species that have been tested are self-compatible, self-fertilization may result (Armbruster, unpubl.). During the pistillate phase only cross-pollination is possible.

Most species of *Dalechampia* are pollinated by female bees that collect the resins secreted by the large secretory glands associated with the staminate flowers (Armbruster & Webster, 1979, 1981, 1982). The amount of resin secreted determines the size of the largest floral visitors. Apparently due to energetic constraints on foraging behavior, only small bees visit *Dalechampia* species that secrete small amounts of resin, whereas large bees (euglossines) visit only those species of *Dalechampia* bearing larger amounts of resin (Armbruster & Webster, 1981, 1982; Armbruster, in prep.).

Because of the viscous, sticky nature of floral resins, it is very difficult to measure the rate of resin secretion. Experimental removal of resin from glands of *D. scandens*, *D. heteromorpha*, and *D. tiliifolia* has shown that resin secretion occurs throughout the period that the bracts are open, and about 0.5–1.5 mm (depth) of resin accumulates across the surface of the gland daily (Armbruster, unpubl.). *Dalechampia dioscoreifolia* appears to follow this pattern as well. Because the rates of secretion are similar in all species studied and because of the difficulties in measuring secretion rates, the area of secretion is probably the best single field measurement of the average quantity of resin available to foraging bees.

The arrangement of the staminate and pistillate flowers also affects the size class of the effective pollinators. Species of *Dalechampia* in which the distances between the gland and the stigmas or the gland and the anthers is relatively large (>ca. 6 mm) are pollinated only by relatively large bees (>ca. 10 mm). Species of *Dalechampia* in which the gland-stigma and gland-anther distances are smaller (<ca. 4 mm) can be pollinated by smaller bees (Armbruster & Webster, 1981, 1982; Armbruster, in prep.).

MATERIALS AND METHODS

Observations on the reproductive biology of *Dalechampia* species were made in the Canal Zone of the Republic of Panama during three

separate periods: 30 June–3 July 1978, 14–18 November 1978, and 9–27 January 1980. Intensive observations were made on three species, *D. dioscoreifolia* Poepp. & Endl., *D. heteromorpha* Pax & Hoffmann (Pax & Hoffmann, 1919; = *D. cissifolia* subsp. *panamensis*, Webster & Burch, 1968; Croat, 1978), and *D. scandens* L., where they occurred together at km 13 Pipeline Road. Intensive observations were also made on *D. dioscoreifolia*, *D. heteromorpha*, and *D. tiliifolia* Lam. where they occurred together at km 15 Pipeline Road. Additional observations were made on these species at 10 other sites in the Canal Zone, including elsewhere along Pipeline Road (as far as Rio Casanga), Madden Dam, Madden Reserve, Barro Colorado Island, and near the Summit Gardens.

For each species we tagged 19–52 inflorescences on 5–7 plants and daily monitored changes in number of staminate flowers open, amount of resin present, and the amount and, when possible, type of pollen on the stigmas. Resin amounts were estimated by observing the depth on the gland. Pollen grains, which are large (ca. 50–150 μm), were counted with the aid of a hand lens; we were able to distinguish between the pollen of *D. tiliifolia* and *D. dioscoreifolia* on the basis of size. *Dalechampia* pollen was distinguishable from pollen of other plants common in the area on the basis of size and color. At half-hour or hour intervals the position of the involucre bracts was assessed. Measurements were made of the gland size and minimum distances between the gland and stigmas, the gland and anthers, and the anthers and stigmas, using dial calipers accurate to 0.05 mm.

Observations on pollinators included counting floral visitors, noting the amount and color of their corbicular/scopal loads, recording their behavior and monitoring their movements. To facilitate these observations some bees were captured, marked on the scutum with correction fluid, and released. Effectiveness of pollinators was determined by monitoring changes in number of pollen grains on the stigmas of each species; effective pollinators (Table 3) are those that were observed to regularly transfer *Dalechampia* pollen to *Dalechampia* stigmas. Visitation rates were calculated for each pollinator species by summing the number of visits observed and dividing by the number of days of observation and by the mean number of inflorescences open in the observation area during the period of observation. Only days in which observations were made

throughout the period of bract opening were included in calculating means. To assess the movement of pollen within and among species, staminate flowers of each species were dusted at short intervals with specific colors of powdered, non-toxic, fluorescent paint; transfer of paint granules was recorded periodically. Vouchers of plant species and floral visitors were collected. In the lab pollen loads were removed from visitors, slides made using Hoyer's medium, and pollen identified with a microscope. Plant vouchers have been deposited at DAV and SCZ.

Experimental intraspecific and interspecific crosses, measures of selfing ability and stigmatic receptivity, and tests of self-compatibility were performed on cultivated material of all four species in the greenhouses at the University of California, Davis from 1975 until 1980. Crosses were made by removing all staminate flowers while in bud and manually transferring pollen with a small camel's-hair brush. Stigma receptivity was tested by pollinating stigmas in emasculated inflorescences at various times during inflorescence development and by testing for peroxidase activity with Peroxtesmo KO paper.

RESULTS

DISTRIBUTION AND FLOWERING TIME

Dalechampia dioscoreifolia, *D. heteromorpha*, *D. scandens*, and *D. tiliifolia* are all locally common in forested and/or open areas of the Canal Zone and other parts of Panama. While at the majority of the 12 study sites only one or two species were present, at two sites we were able to observe three species occurring sympatrically (Table 1). *Dalechampia dioscoreifolia* occurred sympatrically with *D. heteromorpha* at four sites, and with *D. scandens* at three sites. *Dalechampia heteromorpha* occurred with *D. scandens* at one site and with *D. tiliifolia* at two sites. *Dalechampia dioscoreifolia* and *D. tiliifolia* occurred together at one site, but *D. tiliifolia* was restricted to the open scrub, whereas *D. dioscoreifolia* occurred in the forest (Table 1). The two species grew close together only at the ecotone of the forest and scrub communities.

The data on flowering phenology of Panamanian *Dalechampia* are limited; however, it is possible to make a first approximation based on our observations in 1978 and 1980, on available collections, and from the literature. The phenological data presented in Table 2 are based on our observations made in Panama during July, No-

TABLE 3. Floral morphology of Panamanian *Dalechampia*. Numbers in table are means \pm s.d. with N in parentheses.

<i>Dalechampia</i> Species	Number of Sta- minate Flowers	Gland Area (mm ²)	Gland-Stigma Distance (mm)	Gland-Anther Distance (mm)	Anther-Stigma Distance (mm)
<i>D. dioscoreifolia</i>	8-10	30.1 \pm 12.3 (20)	5.5 \pm 1.1 (20)	6.7 \pm 1.5 (10)	10.2 \pm 2.0 (9)
<i>D. heteromorpha</i>	8-10	6.5 \pm 1.8 (16)	3.1 \pm 0.6 (16)	2.2 \pm 0.4 (9)	0.5 \pm 0.6 (9)
<i>D. scandens</i>	9-10	8.7 \pm 3.0 (30)	3.1 \pm 0.8 (29)	2.8 \pm 0.8 (20)	1.8 \pm 0.8 (20)
<i>D. tiliifolia</i>	9-10	22.0 \pm 4.8 (20)	8.9 \pm 1.7 (20)	8.2 \pm 1.0 (15)	3.0 \pm 2.1 (15)

All four of these species set nearly full complements of seeds when inflorescences are manually self-pollinated and screened from pollinators. There are, however, differences among species with respect to the ability of each to self-pollinate and set seed in the absence of pollinators. Observations of pollen movement in a number of species have shown that the distance between the stigmas and the anthers is a primary determinant of the ability of a species to self-pollinate (Armbruster, in prep.). Accordingly, *D. heteromorpha* with a mean anther-stigma distance of only 0.5 mm (Table 3) sets abundant seed in the absence of pollinators. Plants screened from pollinators in greenhouse experiments produce 68% of the maximum possible seedset (N = 279). Manually selfed material had seedsets of 85% of maximum (N = 603), so depression of seedset by the lack of insect-mediated pollination, while significant ($P < 0.001$, $d = 5.90$, normal approximation of binomial distribution; Bailey, 1959), is relatively small.

Dalechampia scandens also has a relatively small mean anther-stigma distance (1.8 mm, Table 3); Panamanian material of this species grown in the greenhouse set abundant seed in the absence of pollinators. A population of *D. scandens* in Costa Rica with a mean anther-stigma distance of 3.6 mm produced 63% of maximum possible seedset (N = 27) when screened from pollinators.

Dalechampia tiliifolia also has a relatively small mean anther-stigma distance (3 mm, Table 3) and self-pollination when pollinators are absent may be relatively frequent. In a population in Costa Rica with a mean anther-stigma distance of 2 mm, inflorescences screened from pollinators produced 93% of maximum possible seedset (N = 84).

Dalechampia dioscoreifolia differs from the other three species in having a relatively large

mean anther-stigma distance (10.2 mm, Table 3). This strongly suggests that self-pollination in the absence of pollinators is rare. In one plant screened from pollinators in the greenhouse only two out of eight inflorescences set seed. A closely related species, *D. aristolochiifolia* H.B.K. has a similar inflorescence morphology (distances between gland-stigma = 5.8 mm, gland-anther = 9.1 mm, anther-stigma = 7 mm; compare with Table 3) and set no seed when grown in the greenhouse and screened from pollinators (N = 108).

FLORAL DEVELOPMENT

The four species of *Dalechampia* considered in this study follow similar patterns of inflorescence development (Table 4). The involucre bracts remain closed when the inflorescences are in bud. On the first day that the bracts open, the stigmas of all four species are receptive. Seed was set in greenhouse material of *D. heteromorpha*, *D. scandens*, and *D. tiliifolia* that was pollinated on the first day of bract opening and subsequently emasculated and screened from pollinators. All four species show positive peroxidase reactions on the first day of bract opening. Similar tests show that the stigmas remain receptive throughout the period of anthesis of the staminate flowers.

Anthesis of the first staminate flower occurs on the second to fourth day after the bracts first open. Each day for the next four to seven days, one to two additional staminate flowers open. Staminate flowers persist two to three days after anthesis and then abscise. Anthesis of the "mature" staminate flower(s) occurs shortly after the bracts open each day (Table 4). In all four species, the anthers dehisce shortly after anthesis.

The involucre bracts open and close in a diurnal cycle characteristic for each of the four species. The bracts of *D. heteromorpha* open daily in the early morning, those of *D. scandens* in the early

TABLE 4. Inflorescence development and behavior. Numbers in columns 1 and 2 are means rounded to the nearest day with range and sample size in parentheses.

Species	Duration of ♀ Phase (days)	Duration of ♂ Phase (days)	Time of Anthesis of Staminate Flowers (hrs)	Period Bracts Are Open (hrs)
<i>D. dioscoreifolia</i>	3 (2-5; 8)	4 (3-6; 4)	ca. 1500	(1400) 1500-1830
<i>D. heteromorpha</i>	3 (2-4; 9)	5 (4-6; 7)	ca. 0700	0600-1900(+)
<i>D. scandens</i>	2 (1-3; 10)	6 (5-6; 8)	ca. 1330	(1300) 1330-1830
<i>D. tiliifolia</i>	2 (1-3; 6)	5 (5-6; 11)	ca. 1430	1400-1800

afternoon, and those of *D. tiliifolia* and *D. dioscoreifolia* in the early to mid-afternoon. The bracts of all four species close shortly after sunset (Table 4).

In all four species, after ca. seven to nine days of receptivity, the inflorescence passes into the fruiting phase. The staminate cycle, including the resin gland, abscises. The bracts in *D. heteromorpha*, *D. scandens*, and *D. tiliifolia* close around the developing capsules. In the last two species the bracts suffuse with chlorophyll. In *D. dioscoreifolia* the bracts abscise when the fruits begin to develop (cf. Armbruster, 1982).

INFLORESCENCE MORPHOLOGY

The basic number and arrangement of staminate and pistillate flowers in the inflorescences is similar in all the four species considered in this study (Table 3, Figs. 1-4). However, there is considerable variation in the color and size of bracts, in the size of the resin glands, and in the distances between floral structures. *Dalechampia heteromorpha* has relatively small green bracts (10-25 mm), and relatively small resin glands (ca. 6.5 mm²), gland-stigma distances (ca. 3.1 mm), and gland-anther distances (ca. 2.2 mm, Table 3). Similarly, *D. scandens* has relatively small, pale-green bracts (10-25 mm), and relatively small resin glands (ca. 8.7 mm²), gland-stigma distances (ca. 3.1 mm) and gland-anther distances (ca. 2.8 mm, Table 3).

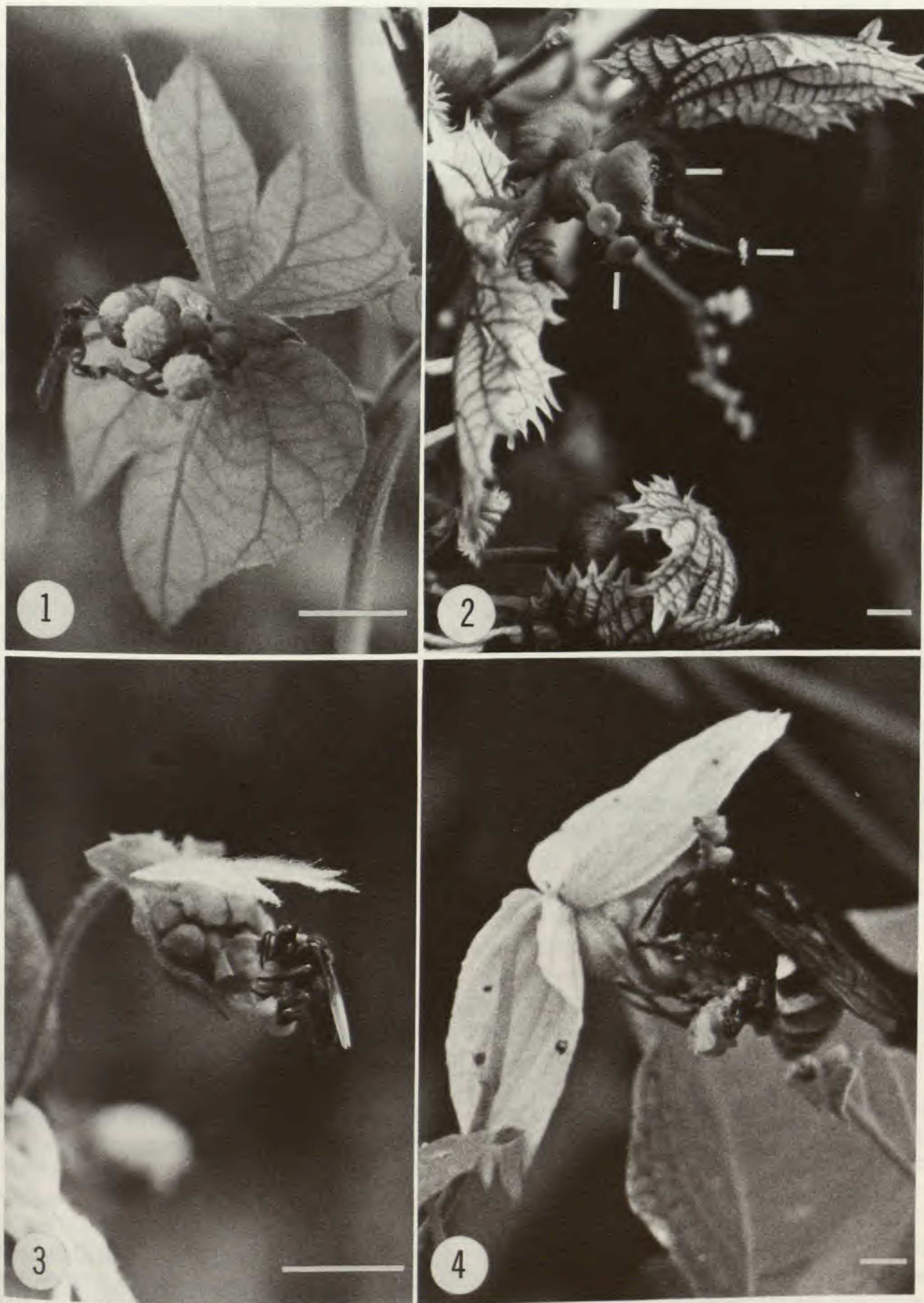
In contrast *D. tiliifolia* has relatively large white bracts (20-50 mm), and relatively large resin glands (ca. 22 mm²), gland-stigma distances (ca. 8.7 mm), and gland-anther distances (ca. 8.2 mm, Table 3). Similarly, *D. dioscoreifolia* has relatively large pink bracts (40-50 mm), relatively large resin glands (ca. 30.1 mm²), and moderately large gland-stigma distances (ca. 5.5 mm), and gland-anther distances (ca. 6.7 mm, Table 3).

The size of the stigmatic tip of the stylar column also varies considerably among the four species. In *Dalechampia heteromorpha* this structure is relatively small (ca. 0.7 mm²); in *D. scandens* it is slightly larger (ca. 0.8 mm²). In *Dalechampia tiliifolia* and *D. dioscoreifolia* the stigmatic tips are considerably larger (ca. 4 mm² and ca. 6 mm², respectively).

POLLINATION AND SEEDSET

As predicted from studies of other species of *Dalechampia* (cf. Armbruster & Webster, 1981, 1982), *D. heteromorpha* and *D. scandens* (both with small resin glands) were visited only by small bees, including *Hypanthidium panamense* and *Trigona* spp. (Table 5). These bees collected resin and/or pollen. We observed no visits by the larger euglossine bees during 42 hours of observation at the Pipeline Road study sites, although these bees were active in the area. Because the gland-stigma and gland-anther distances are small in both of these *Dalechampia* species, the small bees effectively transferred pollen to the stigmas. Pollen was deposited on the legs and ventral surface of the thorax and abdomen. The same species pollinated *D. scandens* and *D. heteromorpha* at other study sites where these plants were observed.

At the Pipeline Road study site, *D. tiliifolia* and *D. dioscoreifolia* were visited and pollinated by medium-sized to large euglossine bees (*Eulaema* spp., *Euglossa bursigera*), which collected resin from the large resin glands (Table 5). Pollen was deposited on the legs and on the ventral surface of the thorax and abdomen. These bee species were observed pollinating *D. tiliifolia* and *D. dioscoreifolia* at a number of different study sites in Panama and also in Costa Rica (Armbruster, unpubl.). Because of the large gland-stigma and gland-anther distances, smaller bees (such



FIGURES 1-4. Panamanian *Dalechampia* and pollinators. Scale bars are 5 mm.—1. *D. heteromorpha* in bisexual condition being visited by *Trigona jaty*.—2. *D. dioscoreifolia* in bisexual condition. Pointers indicate resin gland (top), staminate flower (middle), pistillate flower (bottom).—3. *D. scandens* in bisexual condition being visited by *T. perangulata*.—4. *D. tiliifolia* in bisexual condition being visited by *Eulaema cingulata*.

TABLE 5. Floral visitors to Panamanian *Dalechampia*. Visitation rates based on observations from 9–27 Jan. 1980. Numbers in column 5 are means \pm s.d. with N in parentheses.

<i>Dalechampia</i> Species (Locality)	Floral Visitor (Size in mm)	Effective Polli- nator?	Material Collected	Visitation Rate in Visits · Inflores- cence ⁻¹ · day ⁻¹	Number of Hours of Obser- vation
<i>D. dioscoreifolia</i>					
(km 13, Pipe- line Rd.)	<i>Eulaema cingulata</i> (Fabricius) (22)	+	resin	0.35 \pm 0.47 (4)	8
	<i>Eulaema</i> cf. <i>meriana</i> (Olivier) ^a (24)	+	resin	1.22 \pm 0.80 (4)	8
	<i>Euglossa</i> sp. (11)	+	resin	0.05 \pm 0.08 (4)	8
(km 15, Pipe- line Rd.)	<i>Eulaema cingulata</i> (22)	+	resin	0.81 \pm 0.25 (5)	20
	<i>Euglossa</i> sp. (11)	+	resin	0.08 \pm 0.08 (5)	20
<i>D. heteromorpha</i>					
(km 13, Pipe- line Rd.)	<i>Hypanthidium panamense</i> Cockerell (7)	+	resin and pollen	0.97 \pm 0.48 (3)	42
	<i>Trigona perangulata</i> Cockerell (6)	+	pollen	4.52 \pm 1.54 (3)	42
	<i>Trigona jaty</i> Smith (5)	+	resin	0.05 \pm 0.09 (3)	42
	<i>Trigona fulviventris</i> Guerin (6)	+	pollen	0.02 \pm 0.03 (3)	42
	<i>Trigona</i> sp. (3)	–	resin	0.12 \pm 0.06 (3)	42
<i>D. scandens</i>					
(km 13, Pipe- line Rd.)	<i>Hypanthidium panamense</i> (7)	+	resin and pollen	0.32 \pm 0.26 (3)	42
	<i>Trigona perangulata</i> (6)	+	pollen	5.25 \pm 2.39 (3)	42
	<i>Trigona jaty</i> (5)	+	resin	0.08 \pm 0.14 (3)	42
	<i>Trigona</i> sp. (3)	–	resin	0.10 \pm 0.10 (3)	42
<i>D. tiliifolia</i>					
(km 15, Pipe- line Rd.)	<i>Eulaema cingulata</i> (22)	+	resin	1.31 \pm 0.86 (5)	20
	<i>Euglossa bursigera</i> Moure (11)	+	resin	0.005 \pm 0.012 (6)	20
	<i>Tetrapedia</i> sp. (8)	–	pollen	0.05 \pm 0.07 (5)	20

^a This bee was only observed with binoculars. Due to extreme similarity of mimetic euglossines, we cannot be certain that this is *E. meriana* (cf. Dressler, 1979).

as *Paratetrapedia*, Table 5) are not effective pollinators of *D. tiliifolia* or *D. dioscoreifolia*.

In these four species of *Dalechampia*, a full complement of nine seeds usually develops if pollination is adequate (cf. Armbruster, 1982). There is no evidence suggesting that selective abortion occurs or that, in healthy plants, abscission of inflorescences is due to anything other than lack of pollination. In *D. dioscoreifolia*, of 19 pistillate flowers that had been tagged and monitored and later abscised, 16 (84%) lacked pollen on the stigmas, 3 (16%) had <5 grains per stigma and none had >5 grains per stigma. In *D. scandens*, of 15 monitored inflorescences that abscised, 8 (53%) had <5 grains per stigma, 6

(40%) had between 5 and 10 grains per stigma, and 1 (7%) had >10 grains per stigma.

The proportion of tagged pistillate flowers setting seed varied considerably among species. *Dalechampia heteromorpha* had 100% seedset (N = 30) at km 13 Pipeline Road; at this site *D. scandens* had 76% seedset (N = 87). At km 15 Pipeline Road, *Dalechampia tiliifolia* had 100% seedset (N = 48), whereas *D. dioscoreifolia* had only 42% seedset (N = 24).

POLLINATOR MOVEMENTS BETWEEN SPECIES

At the study site at km 13 Pipeline Road, *D. heteromorpha* and *D. scandens* grew together and were pollinated by the same bee species (Table

5). In the morning hours *Hypanthidium* and *Trigona* visited and pollinated *D. heteromorpha* (Fig. 5). On a number of occasions bees that had just visited *D. heteromorpha* attempted to visit inflorescences of *D. scandens*; however, the bracts of the latter were closed in the morning and successful foraging from, and pollination of, this species was usually not possible before 1300 hrs. Thus there was little potential for interspecific pollen flow in the morning hours.

The majority of attempted visits by *Hypanthidium* and *Trigona* during the morning hours were to *D. heteromorpha*. Out of 599 recorded inflorescence visits during the period from 0800 to 1300 hrs, 535 (89.3%) were successful visits to *D. heteromorpha*, 39 (6.5%) were attempted visits to inflorescences of *D. scandens* that were closed, 13 (2.2%) were visits to old inflorescences of *D. scandens* that had ceased bract movement (and lacked pollen and resin resources), and 12 (2%) were to the rare inflorescences of *D. scandens* that were receptive and slightly open.

In the afternoon (after 1330 hrs) when the inflorescences of *D. scandens* were open, the pollinating bee species "switched" from foraging primarily from *D. heteromorpha* to foraging primarily from *D. scandens*. Of 483 recorded inflorescence visits during the period from 1330 to 1700 hrs, 429 (88.8%) were to *D. scandens* and only 54 (11.2%) were to *D. heteromorpha*. That the bees "preferred" *D. heteromorpha* in the morning and *D. scandens* in the afternoon is statistically highly significant ($P \ll 0.001$, $\chi^2 = 314.4$).

As a consequence of this daily shift in bee preference, the number of interspecific moves by pollinators was surprisingly low. *Dalechampia heteromorpha* and *D. scandens* grew together in the same hedgerow at the km 13 study site; they were frequently intertwined. The inflorescences were of approximately equal number (Table 6) and not spatially segregated to any great extent. Yet out of 576 recorded pollinator moves, only 32 (5.5%) were interspecific (Table 6).

Observations of the movement of paint granules that had been dusted on staminate flowers of both species of *Dalechampia* also suggest a low level of interspecific pollen flow. The frequency was somewhat higher than noted above; 5 (11.6%) of 43 paint transfers were interspecific. [However, the sample size is small and 11.6% is not significantly different from 5.5% (binomial probability, $\beta(5; 43, 0.055) = 0.06$.)] The average distance of paint transfer was 1.45 m ($N =$

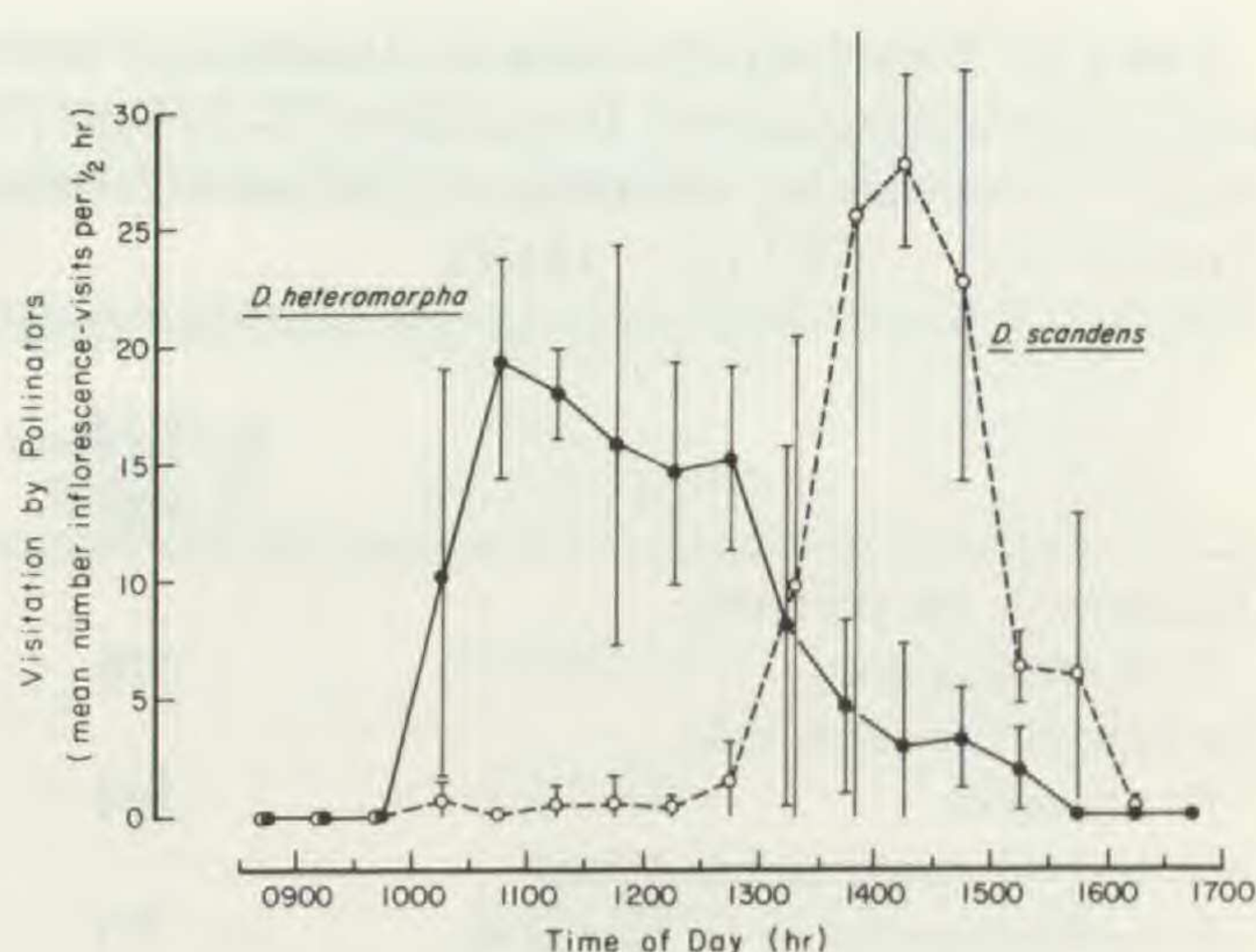


FIGURE 5. Rates of effective visitation by pollinators of *Dalechampia heteromorpha* and *D. scandens* at km 13 Pipeline Road, Canal Zone, Panama, 13-26 January, 1980. Bars are \pm one standard deviation.

24) with a large standard deviation (1.87) and a range of 0.025 m to 7.62 m. Of 27 observed paint transfers in which both the source and destination were known, carry-over of paint (here defined as transfer of paint to inflorescences visited subsequent to the bee's first stop after visiting the source) was observed only twice (=7.4%). Presumably pollen carry-over is correspondingly low (cf. Waser & Price, 1982).

At the study site at km 15 Pipeline Road, *D. tiliifolia* and *D. dioscoreifolia* occurred near one another and were pollinated by the same bee species and individuals. Despite the fact that these two species of *Dalechampia* differ in bract color and morphology and in resin color (*D. tiliifolia*: white bracts, yellow resin; *D. dioscoreifolia*: pink bracts, maroon resin), on many occasions we observed individual *Eulaema cingulata* visit both species "indiscriminately" and to have mixed corbicular loads of yellow and maroon resin. The two plant species were highly segregated. An average of 82 open inflorescences of *D. tiliifolia* were present in an open grassy area, whereas an average of ten open inflorescences of *D. dioscoreifolia* were present at the edge of the forest. Thus even indiscriminate foraging on the part of the bees would result in fewer interspecific moves than would be expected were the plants evenly distributed. Out of 670 recorded moves between inflorescences, 23 (3.4%) were interspecific moves. This is considerably less than would be expected were the plants not spatially segregated (Table 7).

The small proportion of interspecific pollinator moves belies the significance of its effect on

TABLE 6. Observed movements of pollinators between ca. 20 inflorescences of *Dalechampia heteromorpha* and ca. 20 inflorescences of *D. scandens*, 13–26 Jan. 1980, Canal Zone, Panama. Expected values are calculated using 2×2 contingency assuming no pollinator constancy or spatial segregation of plants. Observed differs from expected at $P < 0.001$ ($\chi^2 = 445.9$).

	By <i>Trigona</i> spp.	By <i>Hypan-</i> <i>thidium</i> <i>panamense</i>	Total Observed Pollinator Movements (%)	Total Expected Pollinator Movements
Intraspecific movements: <i>D. heteromorpha</i>	276	58	334 (58.0%)	213
Intraspecific movements: <i>D. scandens</i>	204	6	210 (36.5%)	89
Interspecific movements: From <i>D. heteromorpha</i> to <i>D. scandens</i>	13	2	15 (2.6%)	136
Interspecific movements: From <i>D. scandens</i> to <i>D. heteromorpha</i>	13	4	17 (2.9%)	138

D. dioscoreifolia. A comparison of the number of pollinator moves from inflorescences of *D. tiliifolia* to inflorescences of *D. dioscoreifolia* with the number of intraspecific moves among *D. dioscoreifolia* inflorescences (Table 7), indicates that nearly one-third of the visits to *D. dioscoreifolia* by *E. cingulata* are likely to have resulted in the deposition of pollen of *D. tiliifolia* on the stigmas of *D. dioscoreifolia*. The pollen grains of *D. tiliifolia* are much larger than those of *D. dioscoreifolia*. Stigmas of these two species were examined with a hand lens and pollen grains were identified and counted. All the stigmas examined in inflorescences of *D. dioscoreifolia* that had been visited by a bee coming from *D. tiliifolia* (N = 8) bore large amounts of pollen of *D. tiliifolia*. In two observations of the reverse interspecific move there was no transfer of *D. dioscoreifolia* pollen to the stigmas of *D. tiliifolia*.

The *D. dioscoreifolia* at this locality was thus subject to a substantial influx of pollen from *D. tiliifolia*. Of 15 stigmas of *D. dioscoreifolia* examined on 25 January 1980, 4 (27%) bore pollen of *D. tiliifolia*, 3 (20%) bore pollen of *D. dioscoreifolia*, and 8 (53%) had no pollen on the stigmas. *Dalechampia tiliifolia* at this site was much more abundant (Table 7) and was visited at a higher rate (Table 5). Of 51 stigmas of *D. tiliifolia* examined on 22 January 1980, 42 (82%) bore *D. tiliifolia* pollen and 9 (18%) bore none; no stigmas bore *D. dioscoreifolia* pollen. Thus, at least as compared to *D. tiliifolia*, *D. dioscoreifolia* showed substantial stigmatic contamination by heterospecific pollen and relatively low levels of conspecific pollination. However, part of the latter difference between the two species may be

attributed to the fact that *D. tiliifolia* self-pollinates fairly readily and *D. dioscoreifolia* does not.

HYBRIDIZATION AND INTERSPECIFIC CROSSES

Despite extensive searches in numerous locations in Central and South America, we have never found any evidence of natural hybridization between species of *Dalechampia*. Experimental greenhouse crosses have been performed between *D. scandens* and *D. heteromorpha*. Out of 45 crosses made with *D. scandens* as the pistillate parent, only two produced seed. When these putative hybrids were grown and later selfed, we found that neither the F_1 s nor F_2 s were distinguishable from the pistillate parent; apparently these were the result of pollen contamination from the pistillate parent.

In the reverse cross (*D. heteromorpha* as the pistillate parent), of 51 crosses only three produced seed. These again appeared to be the result of contamination by pollen from the pistillate parent.

It has not been possible to make the combinations of crosses involving the other two species in this study. However, unsuccessful crosses made between four additional Central American species of *Dalechampia* suggest that interspecific incompatibility barriers are common among sympatric species of *Dalechampia*.

Experiments have also been performed to measure how contamination ("clogging") of stigmas with heterospecific pollen affects seedset. In one experiment using *D. scandens* as the pistillate parent, stigmas were pollinated with the pollen of *D. heteromorpha*; two days later they were manually self-pollinated. Other stigmas were

TABLE 7. Observed movements of pollinators between an average of 82 inflorescences of *Dalechampia tiliifolia* and an average of 9.6 inflorescences of *D. dioscoreifolia*, 20–27 Jan. 1980, Canal Zone, Panama. Expected values are calculated using 2×2 contingency assuming no pollinator constancy or spatial segregation of plants. Observed differs from expected at $P < 0.001$ ($\chi^2 = 314.6$).

	By <i>Eulaema cingulata</i>	By <i>Euglossa</i> sp.	Total Observed Pollinator Movements (%)	Total Expected Pollinator Movements
Intraspecific movements: <i>D. tiliifolia</i>	617	1	618 (92.2%)	591
Intraspecific movements: <i>D. dioscoreifolia</i>	27	2	29 (4.3%)	2
Interspecific movements: From <i>D. tiliifolia</i> to <i>D. dioscoreifolia</i>	13	0	13 (1.9%)	40
Interspecific movements: From <i>D. dioscoreifolia</i> to <i>D. tiliifolia</i>	10	0	10 (1.5%)	37

pollinated with a mixture of roughly equal parts of *D. scandens* and *D. heteromorpha* pollen. As a control, stigmas were manually self-pollinated. The results (Table 8) indicate significant depression of seedset (relative to the control) by heterospecific pollination prior to self-pollination ($P < 0.001$). Pollination with the two-species pollen mixture produced significantly more seeds than heterospecific pollination followed by self-pollination ($P < 0.05$). Pollination with the mixture produced fewer seeds than the control treatment, but the difference was not significant ($P = 0.076$).

In a similar experiment on *D. heteromorpha*, the stigmas were pollinated with heterospecific pollen followed by manual self-pollination two days later. The source of heterospecific pollen

was *D. magnistipulata* Webster & Armbruster, a relative of *D. scandens* in sect. *Scandentes*. The control treatment was manual self-pollination. The experimental treatment again resulted in depression of seedset relative to the control ($P < 0.01$, Table 8).

DISCUSSION AND CONCLUSIONS

FLORAL CONSTANCY AND FORAGING STRATEGIES

There is considerable literature indicating that flower constancy is common or even the rule among wild bees (Chambers, 1946; Grant, 1950; Manning, 1956; Sprague, 1962; Free, 1966; Proctor & Yeo, 1972). These authors have suggested that individual bees that learn how to manipulate a flower species will forage most effi-

TABLE 8. Effect of heterospecific pollination on seed production. Numbers in rows 1 and 2 indicate the number of inflorescences in each class. Column 1 differs significantly from column 2 at $P < 0.05$, column 1 from 3 at $P < 0.001$, column 4 from 5 at $P < 0.01$; columns 2 and 3 are not significantly different, $P = 0.076$; χ^2 analysis.

	<i>D. scandens</i> (♀) × <i>D. heteromorpha</i> (♂)			<i>D. heteromorpha</i> (♀) × <i>D. magnistipulata</i> (♂)	
	Heterospecific pollination followed by self-pollination	Pollination with mixture of two pollens	Self-pollination (Control)	Heterospecific pollination followed by self-pollination	Self-pollination (Control)
0–4 seeds produced per inflorescence	26	11	8	8	10
5–9 seeds produced per inflorescence	9	15	34	2	30
Mean number seeds per inflorescence	1.97	3.95	6.93	4.6	8.0

ciently if they restrict their activities to that species, at least as long as it is abundant. Some authors, however, have argued that the foraging strategies of polylectic bees are not adequately described by the concept of simple temporary constancy, but that many bees are inconstant, facultatively constant, or have "majors" and "minors" (e.g., Hobbs, 1962; Macior, 1966; Mosquin, 1971; Heinrich, 1975, 1976b).

The observations on foraging bees made in this study are also inconsistent with the assertion that simple floral constancy is the primary pattern of foraging by bees. We observed numerous individual *Eulaema* foraging from *D. tiliifolia* and *D. dioscoreifolia* without apparent "regard" for species; yet these bees could surely distinguish between these markedly dissimilar *Dalechampia* species. Similarly, we observed individual *Hypanthidium* and *Trigona* on several occasions visit *D. scandens* and *D. heteromorpha* indiscriminately, moving to nearest neighbors as encountered on their foraging routes.

Yet bees did distinguish between species of *Dalechampia* under certain conditions. *Trigona* and perhaps *Hypanthidium* appeared to distinguish between *D. scandens* and *D. heteromorpha* when there were differences in the available resources. When inflorescences of *D. scandens* were closed in the morning and pollen and resin resources were unavailable to foraging bees, *Trigona* and *Hypanthidium* foraged from *D. heteromorpha* on 89.3% of the inflorescence visits (N = 599). In the afternoon when the pollen and resin resources were depleted in *D. heteromorpha*, these same bee species foraged "preferentially" from *D. scandens*, visiting this species on 88.8% of all inflorescence visits (N = 483).

Similar observations were made by Armbruster and Webster (1982) on the behavior of *Hypanthidium* nr. *melanopterum* foraging on *Dalechampia scandens* and *D. affinis* Muell.-Arg. in Brazil. In this community *D. scandens* opened in the morning and *D. affinis* opened in the afternoon. In the morning *Hypanthidium* visited only *D. scandens*; of 19 visits observed prior to 1400 hrs, all were to *D. scandens*. In the afternoon, after the inflorescences of *D. affinis* opened and the pollen and resin resources of *D. scandens* were depleted, the same individual bees "preferentially" visited *D. affinis*; after 1430 hrs 21 (84%) of 25 observed visits were to *D. affinis* even though inflorescences of *D. scandens* were still open (cf. Fig. 2 in Armbruster & Webster, 1982).

When there are differences in the resource available, euglossine bees, as well, forage preferentially from one species of *Dalechampia* over another. It has been pointed out several times that euglossine bees (of medium to large size) collect resin preferentially from *Dalechampia* species with large resin glands, "ignoring" those species with smaller glands (Armbruster & Webster, 1981, 1982). This behavior was exhibited during this study as well.

Thus it appears that at least some species of the diverse genera *Eulaema*, *Euglossa*, and *Hypanthidium* employ a "strategy" of facultative constancy which "maximizes" resource harvest. They do not discriminate between similar flower species when there is no advantage in doing so. However, these bees do discriminate between similar flower species when they perceive that there are differences between them in the resources available. Zimmerman (1981) has suggested that bumblebees employ this same strategy, and Simpson and Neff (1981) have drawn similar conclusions from their studies of *Centris* foraging oils in Texas. This pattern may also hold for individual *Trigona* (a social species); however, because of the possibility of sequential foraging on different *Dalechampia* species by different workers from the same hive, many more marked individuals need to be observed.

REPRODUCTIVE INTERACTIONS BETWEEN PLANT SPECIES

Recently there has been considerable interest in the nature of reproductive interactions between sympatric plant species (Waser, 1983). Under certain conditions, co-occurring plant species may mutualistically facilitate each other's reproduction (Macior, 1971; Brown & Kodric-Brown, 1979; Waser & Real, 1979; Schemske, 1981). Perhaps more common, however, is reproductive interference between co-occurring species. Reproductive interference is manifested in several ways. Simultaneously flowering sympatric species may compete for pollinator service if pollinators are not abundant enough to effect full pollination of all flowers of both species (Levin, 1970; Levin & Anderson, 1970; Mosquin, 1971). If a pollinator is constant and prefers one species over another, the second species will suffer from lower rates of pollination as a consequence of its sympatry with the first species. Even if a pollinator does not "prefer" one flower species over another, both species may

have lower rates of effective pollination as a result of the large number of wasted interspecific pollinator moves. This has especially dire consequences on the numerically minor species (Levin & Anderson, 1970; cf. Lewis, 1961).

Another detrimental effect may accrue from sharing pollinators even when pollinators are sufficiently abundant to adequately pollinate all flowers of both species. If shared pollinators results in interspecific pollen flow, the reproductive fitness of sympatric plants may be depressed in several ways. If the species are cross-compatible but produce sterile hybrids, reproductive fitness is lowered and severe selection operates against individuals sharing pollinators (Lewis, 1961; Grant, 1966). Interspecific pollination also represents a major loss of genomic copies (pollen); any plant that is effective in getting its pollen to conspecific stigmas will be at a substantial selective advantage (Charnov, 1979). We have presented evidence of a third consequence of interspecific pollen flow: seedset is depressed by the presence of heterospecific pollen on stigmas, even if there is adequate conspecific pollination (also cf. Waser, 1978a, 1978b; Sukada & Jayachandra, 1980; Thomson et al., 1981). One or several of these processes presumably generates selective pressures that may lead to partitioning of pollinator resources by coexisting plant species, and thereby reduction of competition for pollinator service and/or reduction of interspecific pollen flow.

Several of these selective pressures may be operating in assemblages of *Dalechampia* species. We have shown that one consequence of pollinator sharing by *D. tiliifolia* and *D. dioscoreifolia* is substantial interspecific pollen flow, and that interspecific pollen flow between *D. scandens* and *D. heteromorpha* can reduce the number of seeds produced by members of both species. It thus seems likely that populations of sympatric species will have adapted to coexistence with their congeners, at least if their ranges overlap substantially and they have co-occurred for a sufficiently long period of time. Previous studies of two-species assemblages of *Dalechampia* supported this expectation (Armbruster & Webster, 1979, 1981, 1982). In the present study we found that most of the coexisting species partition pollinators in ways that result in low levels of interspecific pollen flow. At km 13 Pipeline Road, *D. dioscoreifolia* was the only species that produced large quantities of resin and had relatively large interfloral distances; it alone was pollinated by

euglossine bees. *Dalechampia heteromorpha* and *D. scandens*, with smaller resin glands and smaller interfloral distances were not visited by euglossines, but instead were pollinated by small megachilid and meliponine bees. Although these two species were visited by the same bee species and individuals, the levels of interspecific bee movement, and presumably pollen flow, were relatively low; *D. heteromorpha* was pollinated primarily in the morning, *D. scandens* in the afternoon.

Dalechampia tiliifolia and *D. heteromorpha* occurred together at several sites. These species utilized different pollinators as well; *D. tiliifolia* was pollinated by euglossine bees, *D. heteromorpha*, again, by megachilid and meliponine bees. We did not observe *D. tiliifolia* and *D. scandens* growing together in Panama. It is possible that they do occasionally occur together; if so, they probably do not share pollinators.

At km 15 Pipeline Road, we observed *D. tiliifolia* and *D. dioscoreifolia* growing together. Both species have large resin glands and relatively large interfloral distances; they are both pollinated by species of euglossine bees. The most frequent pollinator of these two species at this site, *Eulaema cingulata*, moved between the two species with sufficient frequency to effect considerable interspecific pollination.

Dalechampia dioscoreifolia was less abundant than *D. tiliifolia* at this site (with averages of ten and 82 inflorescences, respectively). As a consequence it was subject to substantial pollen flow from *D. tiliifolia* and must have lost much pollen to foreign stigmas. The effects of interspecific pollination on *D. tiliifolia* were diluted among a larger number of inflorescences and were probably of minor significance.

This relationship may have detrimentally affected the reproductive output of individuals of *D. dioscoreifolia* at this site. With respect to the male component of fitness, probably over 25% of the pollen was lost to heterospecific stigmas during our study (Table 7). The female component of fitness may also have been affected; a substantial proportion of the monitored stigmas of *D. dioscoreifolia* bore alien pollen (e.g., 27% on 25 Jan. 1980). We lack data on the effect of alien pollen on the seedset of *D. dioscoreifolia*, but the effect may be similar to that on other *Dalechampia* species. In *D. scandens* and *D. heteromorpha* there was marked depression of seedset if alien pollen reached the stigmas first; however, these two species have smaller stigmas and

may be more sensitive to stigma contamination and/or stylar "clogging" than *D. dioscoreifolia*.

Only a small proportion of the stigmas of *D. dioscoreifolia* at km 15 bore significant amounts of conspecific pollen (e.g., 20% on 25 Jan. 1980). Those stigmas lacking conspecific pollen were either devoid of pollen (53%, 25 Jan. 1980) or bore pollen of *D. tiliifolia* (27%, 25 Jan. 1980). This suggests that effective pollinator service was in short supply; in view of the rarity of self-pollination in *D. dioscoreifolia*, reduced pollinator service probably resulted in reduced seed production.

There is some evidence that *D. dioscoreifolia* suffered from lower rates of effective pollination as a result of its proximity to *D. tiliifolia*. Nearly one-third of the pollinator visits to *D. dioscoreifolia* were "wasted," bringing loads of *D. tiliifolia* pollen. When we factor the "wasted" visits out of the visitation rates, we find that *D. dioscoreifolia* at km 15 Pipeline Road had significantly lower rates of effective visitation than did *D. dioscoreifolia* at km 13 Pipeline Road. During three hours of observation on each of two days when the number of open inflorescences were the same in the two populations, we observed 19 visits by *Eulaema cingulata* and 24 visits by *E. cf. meriana* at km 13; at km 15 we observed only ten visits by *E. cingulata*, of which one-third could be expected to be ineffective. Thus the rate of effective visitation to *D. dioscoreifolia*, even by *E. cingulata* alone, was significantly lower at km 15 than at km 13 ($7 < 19$, $P < 0.015$, assuming Poisson distribution, Pearson & Hartley, 1958).

Additional evidence suggests that *D. dioscoreifolia* was at a competitive disadvantage relative to *D. tiliifolia* at the Pipeline Road study site, and that this contributed to lower rates of pollinator visitation. If bees visit these two species without preference and without regard to the spatial distribution of the two species, we would expect that the number of visits to each species would be proportional to the number of open inflorescences of each species. The frequency of visits to *D. tiliifolia*, then, should have been 0.895 (its average floral frequency) and the frequency of visits to *D. dioscoreifolia* should have been 0.105. The observed frequencies of visits were 0.937 and 0.063 respectively, which are significantly different from the expected at $P < 0.001$ ($N = 670$; normal approximation of binomial distribution; Bailey, 1959). Thus the rate of visitation to *D. dioscoreifolia* is significantly lower

than expected; apparently the bees either have a weak "preference" for *D. tiliifolia* or they are foraging in a manner that causes them to encounter *D. tiliifolia* more frequently.

The expected consequence of sharing pollinators with *D. tiliifolia* is reduced seedset in *D. dioscoreifolia*. Seedset is much lower in the population of *D. dioscoreifolia* at km 15 Pipeline Road than is the seedset for other species. However, the truly critical data are lacking. We have only subjective comparisons between populations of *D. dioscoreifolia*; the population of *D. dioscoreifolia* at km 15 Pipeline Road appeared to produce less fruit than did the populations of similar size we observed at km 13 Pipeline Road, and on Barro Colorado Island, where *D. tiliifolia* was absent.

A puzzling question emerges from this study. There appears to be ample evidence of selective disadvantage to individual plants sharing pollinators and exchanging pollen with members of other species. Most species of *Dalechampia* considered in this study appear to be adapted (or preadapted) to coexisting with each other. *Dalechampia tiliifolia* and *D. dioscoreifolia*, however, share pollinators, exchange pollen, and do not appear to be adapted to coexistence.

The adaptive explanation of pollinator sharing leading to higher rates of pollination for relatively rare or few-flowered species (Schemske, 1981) does not seem applicable here because both species of *Dalechampia* are fairly common and produce relatively large numbers of flowers; also *D. dioscoreifolia* appears to have suffered reduced rates of effective pollination and possibly lower reproductive output as a consequence of its proximity to *D. tiliifolia*. Instead, the explanation may be that these two species are not adapted to coexistence because they rarely occur together. We have observed *D. tiliifolia* at 14 sites and *D. dioscoreifolia* at nine sites in Central and South America (Armbruster, unpubl.), but only at the Pipeline Road site were the two species growing together. The two species usually occur in different habitats; in Panama *D. dioscoreifolia* occurs predominately in forest, and *D. tiliifolia* occurs predominately in open scrub (Table 1). Thus the distribution of these two species is better described as parapatric than as sympatric. Since reproductive interference impacts only a very small peripheral segment of the population of *D. dioscoreifolia*, there would not occur population-wide evolutionary adjustments to sympatry with *D. tiliifolia*. Local adaptation would

be possible only if gene flow were very localized, which seems unlikely in this species (cf. Janzen, 1971).

RESOURCE PARTITIONING AND COMMUNITY STRUCTURE

The four species of *Dalechampia* we observed in Panama may be an important part of this tropical forest ecosystem. While the flowers provide resin resources for only four genera of bees, these genera are themselves sufficiently abundant to be important pollinators of many other tropical plants (cf. Gilbert, 1980). Female euglossine bees visit a large variety of plants for nectar and pollen resources, while the males visit and pollinate dozens of species of orchids (Ackerman, 1984; Dressler, 1982). Similarly, *Trigona* and *Hypanthidium* visit numerous other plant species for pollen and nectar. We observed both *Trigona* and *Hypanthidium* visiting a number of weedy roadside species in our study areas.

Most of the literature addressing pollination at the community level concludes that plant species that coexist in stable communities occupy different "pollination niches" (Levin, 1970; Levin & Anderson, 1970; Mosquin, 1971; Frankie, 1975; Heinrich, 1975, 1976; Reader, 1975; Stiles, 1975, 1977; Feinsinger, 1978; Waser, 1978). However, some authors suggest that niche separation is not the only expected outcome of ecological processes (Brown & Kodric-Brown, 1979; Grant & Grant, 1968; Proctor & Yeo, 1972; Macior, 1971; Schemske, 1981), and others argue that observing niche separation in a single community does not demonstrate that any ecological or evolutionary processes have occurred (Connor & Simberloff, 1979; Strong et al., 1979; Poole & Rathcke, 1979; Waser, 1983).

Most of the species of *Dalechampia* that occur together at our study sites in Panama are either pollinated by different bees or are pollinated at different times of the day. This is consistent with theoretical expectations. The only exception, pollinator sharing between *D. dioscoreifolia* and *D. tiliifolia*, may be a case of two species lacking adaptation for sympatry because they rarely occur together; when they do occur sympatrically it may impact only a small portion of each population. If so, this is compatible with the resource-partitioning theory as well. Before we can make strong claims of community organization, however, it will be necessary to collect more data on the relative frequency of co-occurrence of species, pollen-flow dynamics, reproductive con-

sequences of interspecific pollination, and comparative reproductive performance of populations of each species as they occur with and without sympatric congeners. Especially useful would be establishment of experimental populations of *D. tiliifolia* and *D. dioscoreifolia* in varying ratios, to determine the effects of sympatry on pollination rates and reproductive performance.

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